

Studies on Olividae. VIII. Protoconch Measurements as Supraspecific Characters in the Family Olividae

by

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Abstract. Data on 87 taxa indicate that protoconch measurements are efficient supraspecific characters in the family Olividae.

INTRODUCTION

Olive shells are difficult to describe in words because they do not possess obvious, clear-cut conchological discriminating features. They are devoid of sculpture and many are of rather uniform shape. Columellar plications are often quite complex, irregular in shape, and variable. When present, color patterns are often highly variable and their intricacy defies accurate verbal description. In some cases the worded descriptions utilized so far do not transmit relevant taxonomic information. Without reference to types or illustrations many species of *Oliva* simply cannot be unambiguously recognized from their original description (often written in the language of the art critic rather than that of the scientist). In addition, the great variability of many olive shells is a familiar problem to malacologists: it is often difficult to draw sharp and stable boundaries between taxa.

The problems prevailing at the species level are logically expected to be reflected at the upper taxonomic levels. There has been no recent critical review of the supraspecific grouping of the family Olividae as a whole. For lack of better choice, the divisions adopted in the latest revision (PETUCH & SARGENT, 1986) have been followed hereunder.

As long as objective discriminant characters (and the limits of their variation) are not clearly defined, the classification of Olividae is bound to remain largely a question of personal opinion. The use of reliable, quantitative characters would certainly help to clear some of that systematic confusion. In an attempt to provide such taxonomic tools, a set of 13 protoconch measurements has been defined by TURSCH & GERMAIN (1985, 1986a) together with some other quantitative shell characters. These protoconch characters have been shown to be useful and reliable both at the subspecific (TURSCH *et al.*, 1986a) and the specific

(TURSCH *et al.*, 1986b) levels in the genus *Oliva*. No data justifying their use at the supraspecific level have been provided so far.

Protoconch measurements cannot always be utilized as identification characters because the apex of many olive shells is quite fragile and often found missing or damaged (this is probably due to rough handling as the percentage of shells with intact protoconch is much higher in self-collected material than in museum or commercial specimens). On the other hand, protoconch data do not vary with the size of the specimen. They allow easy comparison of adult with juvenile shells, can be utilized for fossil material, and are thus very attractive for systematic work.

The taxonomic importance of the protoconch has not escaped the notice of other students of Olividae. In their recent revision of the genus *Oliva*, PETUCH & SARGENT (1986) state: "Because this is such a specific character, the protoconch should be considered the most important means of differentiating species within genus and subgenus groups." Very brief references to the size (and sometimes the general shape) of the protoconch can indeed be found for 22 of the 176 taxa described in that work. Protoconch characters have also been utilized at the specific level in the genus *Agaronia* (LOPEZ *et al.*, 1988).

Can protoconch measurements be utilized at the supraspecific level in the family Olividae? The statement of PETUCH & SARGENT (1986) reproduced here above explicitly restricts the use of protoconch characters to the specific level. The authors do not use these characters in the definition of any of the 19 subgenera (10 being newly created) they recognize in the genus *Oliva*. On the other hand, protoconch size has been utilized as a supraspecific character in Ancillinae by KILBURN (1977). The general uniformity of the protoconch within the genus *Ancilla* is also reported (and illustrated for many species) by KILBURN (1981).

The present work is a preliminary survey of protoconch morphology trends in the family Olividae. Its sole purpose is to test the taxonomic potential of some protoconch measurements as supraspecific characters in the family Olividae.

MEASUREMENTS

In order to keep this paper within reasonable size limits, only three very simple measurements (**nw**, **lpro**, **spro**) have been utilized. These measurements are justified and defined in detail in TURSCH & GERMAIN (1985). All protoconch measurements are performed using a dissecting microscope at suitable magnification. The measurement **nw** is the number of volutions of the protoconch. The transition from protoconch to teleoconch is carefully determined and marked with removable ink. The determination of the transition is straightforward in most *Oliva* but sometimes more difficult in other groups. Discontinuities in the suture and changes of curvature of the whorl are then of great assistance. The shell is then properly oriented and the angular position of the mark relative to the reference axes of the ocular reticulum is easily determined to the nearest 18°. The quantity **nw** can thus be measured to the nearest 0.05 whorl. The suture of the early whorls is then carefully drawn with the help of the camera lucida attachment of the microscope. A 1-mm reference length (predetermined on the ocular reticulum) is also drawn. The measurements **spro** (the diameter of the nucleus) and **lpro** (the diameter of the protoconch at one and one-half volution) are thus easily made. The meaning of **lpro** and **spro** is evident from Figure 1. The quantity (**lpro** - **spro**) reflects the rate of expansion of the spiral in the plane perpendicular to the axis of the shell. The quantities **nw** and (**lpro** - **spro**) are *a priori* independent characters.

One will note that the above protoconch measurements differ from some in common use. The choice of the method, its accuracy, and precision are discussed in TURSCH & GERMAIN (1985). One will also note that the above measurements determine neither the shape nor the size of the protoconch.

MATERIAL EXAMINED

In the genus *Oliva* 47 species were selected at random with the only constraint being that 12 taxa (26%) were chosen in the Panamic-Atlantic region, in order to approximate the real distribution of species (Table 1). Species from that zone amount to 14 (25%) of the 57 species recognized by ZEIGLER & PORRECA (1969) and 43 (24%) of the 176 species recognized by PETUCH & SARGENT (1986). In the other genera, selection of the sample was very much influenced by the availability of specimens with the protoconch intact. The problem was often compounded by the fact that the protoconch of many species is very difficult to measure; these taxa were not considered. The initial aim was to measure five specimens of every species. This

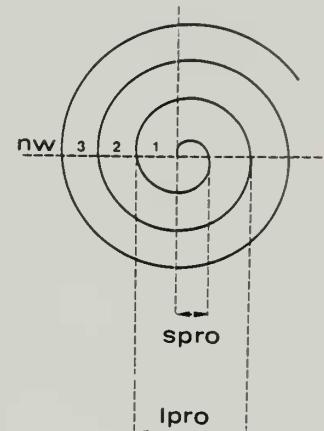


Figure 1

Top view of a fictive protoconch: **nw**, **lpro**, and **spro**.

could not always be achieved for lack of available intact specimens.

The list hereunder does not endorse the correctness and the validity of all the taxa. Some names are used with great reluctance.

Abbreviations: AM, refers to specimens from the Instituut voor Taxonomische Zoölogie (Zoölogische Museum, Amsterdam); DG, to the D. Greifeneder collection (Schwenningen); FN, to the F. Nolf collection (Ostende); JS, to the J. Senders collection (Brussels); RM, to the R. Martin collection (Cebu); and BT, to the B. Tursch collection (Brussels).

Subfamily OLIVINAE

Genus Agaronia

A. acuminata boavistensis Burnay & da Conceição, 1986. CABO VERDE: BT-1212 (Sal Rei, Boavista I.), BT-5893, BT-5894, and BT-5896 (no loc.). *A. propatula* Conrad, 1849. COSTA RICA (Playa de Jascos): BT-5897, BT-5898, BT-5899, and BT-5900. *A. travassosi* Lange de Morretes, 1938. BRASIL (off Cabo Frio): BT-2926, BT-3270, BT-3277, and BT-4070.

Genus Oliva

O. amethystina Röding, 1798. For this species see TURSCH *et al.*, 1986b. AUSTRALIA (Queensland, Bowen): DG-3670/5; PHILIPPINES: DG-0253 (Sulu) and DG-0995 (Cebu); SOLOMONS (Langa-Langa): DG-2525/6; TAHITI (Faaone): DG-1719/b. *O. arcuata* Marrat, 1871. THAILAND: BT-1232 and BT-0081 (no loc.); BT-3940 and BT-3942 (off Ranong); BT-3947 (off Kor Raya Is.). *O. australis* Duclos, 1835. S. AUSTRALIA: BT-1475 and BT-1478 (no loc.); BT-3603 (Elliston Bay); BT-4506 (Yorke Peninsula); BT-3600 (Brighton Reef). *O. buelowi* Sowerby, 1888. PAPUA NEW GUINEA (Hansa Bay, Laing Is.): BT-0422, BT-0423, BT-0424, BT-0425, and BT-0426. *O. bulbiformis* Duclos, 1835. INDONESIA (Bali): JS-028, JS-029, BT-1549, and BT-1551. PHILIPPINES (Bohol): BT-1556. *O. bulbosa* Röding, 1798. ABU DHABI: BT-4604, BT-4605, BT-4606, BT-4607, and BT-4608. *O. caerulea* Röding, 1798. INDONESIA (Bali): BT-0451, BT-

Table 1
Taxa examined.

Subfamily OLIVINAE
Genus <i>Agaronia</i>
<i>A. acuminata boavistensis</i> Burnay & da Conceição, 1986.
<i>A. propatula</i> Conrad, 1849.
<i>A. travassosi</i> Lange de Morretes, 1938.
Genus <i>Oliva</i>
<i>O. amethystina</i> Röding, 1798.
<i>O. arctata</i> Marrat, 1871.
<i>O. australis</i> Duclos, 1835.
<i>O. buelowi</i> Sowerby, 1888.
<i>O. bulbiformis</i> Duclos, 1835.
<i>O. bulbosa</i> Röding, 1798.
<i>O. caerulea</i> Röding, 1798.
<i>O. caldania</i> Duclos, 1835.
<i>O. carneola</i> Gmelin, 1791.
<i>O. caroliniana</i> Duclos, 1835.
<i>O. concinna</i> Marrat, 1871 (of authors).
<i>O. dubia</i> Schepman, 1911.
<i>O. flammulata</i> Lamarck, 1811.
<i>O. hirasei</i> Kuroda & Habe, 1952.
<i>O. fulgorator</i> Röding, 1798.
<i>O. kaleontina</i> Duclos, 1835.
<i>O. lacanentai</i> Greifeneder & Blöcher, 1985.
<i>O. lenhilli</i> Petuch & Sargent, 1986.
<i>O. lignaria</i> Marrat, 1868.
<i>O. mantchora</i> Duclos, 1835.
<i>O. miniacea</i> Röding, 1798.
<i>O. neostina</i> Duclos, 1835.
<i>O. oliva</i> L., 1758 (of authors).
<i>O. ornata</i> Marrat, 1867.
<i>O. parkinsoni</i> Prior, 1975.
<i>O. Paxillus</i> Reeve, 1850.
<i>O. polypasta</i> Duclos, 1835.
<i>O. porphyria</i> L., 1758.
<i>O. reclusa</i> Marrat, 1871.
<i>O. reticularis</i> Lamarck, 1811.
<i>O. reticulata</i> Röding, 1798.
<i>O. rubrolabiata</i> Fischer, 1902.
<i>O. rubrofulgorata</i> Schepman, 1911.
<i>O. rufula</i> Duclos, 1835.
<i>O. sayana</i> Ravenel, 1834.
<i>O. scripta</i> Lamarck, 1811.
<i>O. semmelincki</i> Schepman, 1911.
<i>O. sericea</i> Röding, 1798.
<i>O. sidelia</i> Duclos, 1835.
<i>O. spicata</i> Röding, 1798.
<i>O. splendidula</i> Sowerby, 1825.
<i>O. taeniata</i> Link, 1807.
<i>O. tessellata</i> Lamarck, 1811.
<i>O. tricolor</i> Lamarck, 1811.
<i>O. undatella</i> Lamarck, 1811.
<i>O. vidua</i> Röding, 1798.
<i>O. williamsi</i> Melvill & Standen, 1897.
Genus <i>Olivancillaria</i>
<i>O. contortuplicata</i> Reeve, 1850.
<i>O. urceus</i> Röding, 1798.
<i>O. uretai</i> Klappenbach, 1965.
<i>O. vesica vesica</i> Gmelin, 1791.
Subfamily OLIVELLINAE
Genus <i>Olivella</i> s.l.
<i>O. anazora</i> Duclos, 1835.

Table 1 Continued.
<i>O. gracilis</i> Broderip and Sowerby, 1829.
<i>O. japonica</i> Pilsbry, 1895.
<i>O. pulchella</i> Duclos, 1835.
<i>O. volutella</i> Lamarck, 1811.
<i>O. zanoeta</i> Duclos, 1835.
<i>O. zonalis</i> Lamarck, 1811.
Subfamily ANCILLINAE
<i>Ancilla</i> (<i>Sparellina</i>) <i>acuminata</i> Sowerby, 1859.
<i>Ancilla</i> (<i>Sparellina</i>) <i>ampla</i> Gmelin, 1791.
<i>Baryspira australis</i> Sowerby, 1830.
<i>Ancillus buccinoides</i> Lamarck, 1803.
<i>Ancillarina canalifera</i> Lamarck, 1802.
<i>Ancilla</i> (<i>Sarella</i>) <i>castanea</i> Sowerby, 1830.
<i>Ancillista cingulata</i> Sowerby, 1830.
<i>Ancilla cinnamomea</i> Lamarck, 1801.
<i>Baryspira depressa</i> Sowerby, 1859.
<i>Amalda</i> (?) <i>dimidiata</i> Sowerby, 1850.
<i>Alocospira</i> (?) <i>edithae</i> Pritchard & Gatliff, 1898.
<i>Eburna glabrata</i> L., 1758.
<i>Eburna lienardi</i> Bernardi, 1821.
<i>Ancilla</i> (<i>Sparellina</i>) <i>lineolata</i> A. Adams, 1853.
<i>Alocospira</i> (s.l.) <i>marginata</i> Lamarck, 1810.
<i>Ancilla</i> (<i>Hesperancilla</i>) <i>matthewsi</i> Burch and Burch, 1967.
<i>Alocospira</i> (s.l.) <i>monilifera</i> Reeve, 1864.
<i>Ancillista muscae</i> Pilsbry, 1826.
<i>Gracilispira novaezelandiae</i> Sowerby, 1859.
<i>Ancilla</i> (<i>Sparellina</i>) <i>ovalis</i> Sowerby, 1859.
<i>Ancillus olivula</i> Lamarck, 1803.
<i>Alocospira</i> (s.l.) <i>rosea</i> Macpherson, 1951.
<i>Ancilla</i> (<i>Sarella</i>) <i>sarda</i> Reeve, 1864.
<i>Amalda tankervillii</i> Swainson, 1825.
<i>Ancillista velesiana</i> Iredale, 1936.
<i>Ancilla</i> (<i>Sarella</i>) <i>ventricosa</i> Lamarck, 1811.

0452, BT-0454, BT-455, and BT-1987. *O. caldania* Duclos, 1835. AUSTRALIA (Queensland, no loc.): BT-1607, BT-1609, BT-1611, BT-1612, and BT-1614. *O. carneola* Gmelin, 1791. SOLOMON Is.: BT-0301 (Guadalcanal); BT-2516 (Langa-langa); BT-2548, BT-2549, and BT-2553 (no loc.). *O. caroliniana* Duclos, 1835. MOZAMBIQUE (no loc.): BT-1567. SOUTH AFRICA (Durban): BT-2617, BT-2618, BT-3800, and BT-3997. *O. concinna* Marrat, 1871 (of authors). This is the taxon figured pl.10, figs. 9 and 10 in PETUCH & SARGENT (1986) and pl.10, fig. 3 in ZEIGLER & PORRECA (1969). NEW HEBRIDES (Port Vila): BT-4343. SOLOMONS: BT-2440 and BT-2441 (Honiara); BT-4438 (Guadalcanal); BT-4342 (no loc.). *O. dubia* Schepman, 1911. PAPUA NEW GUINEA (Hansa Bay, Laing Is.): BT-4928, BT-4929, BT-4930, and BT-4931. PHILIPPINES (Bohol): RM-0017. *O. flammulata* Lamarck, 1811. GABON (Port Gentil): BT-2087 and BT-2088. MAURITANIA (La Awera): BT-4215. SENEGAL (Dakar): BT-2127 and BT-4432. *O. fulgorator* Röding, 1798. ARUBA: AM-10, AM-33, and AM-11 (no loc.); BT-3420 (off Malmok). VENEZUELA (La Guayra): Am-01. *O. hirasei* Kuroda & Habe, 1952. PHILIPPINES (Sulu): BT-5021, BT-5022, BT-5023, BT-5024, and BT-5025. *O. kaleontina* Duclos, 1835. GALAPAGOS (St. James): BT-4225. PANAMA (Cebaco Is.): BT-3751, BT-3752, BG-3753, and BT-3756. *O. lacanentai* Greifeneder & Blöcher, 1985. PHILIPPINES (off Cebu, 250–300 m): BT-5045, BT-5046, BT-5047, BT-5048, and BT-5049. *O. lenhilli* Petuch & Sargent, 1986. PHILIPPINES (off Bohol, 100 m): RM-003, RM-005, RM-006, RM-008, and RM-009. *O. lignaria* Marrat, 1868. W.

AUSTRALIA: BT-4831 and BT-4832 (Northwest Cape); BT-3206, BT-3207, and BT-3208 (Broome). *O. manitichora* Duclos, 1835. For this species see TURSCH et al., 1986b. MALDIVES (Ihuru reef): DG-5107/3. PAPUA NEW GUINEA (Port Moresby): DG-5408/3 and DG-5408/8. PHILIPPINES (no loc.): BT-4534 and BT-4545. *O. miniacea* Röding, 1798. PHILIPPINES (no loc.): BT-3678, BT-4585, BT-4586, BT-4587, and BT-4588. *O. neostina* Duclos, 1835. PAPUA NEW GUINEA (Hansa Bay): BT-5016, BT-5017, BT-5018, BT-5019, and BT-5020. *O. oliva* L., 1758 (of authors). This is the taxon figured pl.15, figs. 14 and 15 in PRETUCH & SARGENT (1986). PHILIPPINES (no loc.): BT-4589, BT-4590, BT-4591, BT-4592, and BT-4593. *O. ornata* Marrat, 1867. PHILIPPINES: FN-64/1 and BT-0387 (no loc.); BT-4243 and BT-4837 (Sulu). *O. parkinsoni* Prior, 1975. SOLOMONS (no loc.): BT-2480, BT-2481, BT-2482, BT-2483, and BT-2485. *O. paxillus* Reeve, 1850. HAWAII: BT-0931 and BT-1928 (Oahu); BT-1931 (Kauai); BT-4314 and BT-4316 (no loc.). *O. polpasta* Duclos, 1835. MEXICO: BT-4613 (Oaxaca, off Salina Cruz); BT-0314, BT-0315, and BT-0316 (Baja California). PANAMA (Kobbe Beach): BT-0363. *O. porphyria* L., 1758. PANAMA (Cebaco Is.): BT-3717, BT-3722, BT-3723, BT-3724, and BT-3726. *O. reclusa* Marrat, 1871. ARUBA (Hadicurari Beach): AM-020, AM-021, AM-022, AM-023, and AM-025. *O. reticularis* Lamarck, 1811. CUBA (Guantanamo): BT-2190, BT-2220, BT-2221, BT-2223, and BT-2666. *O. reticulata* Röding, 1798. PHILIPPINES (no loc.): BT-4594, BT-4595, BT-4596, BT-4597, and BT-4598. *O. rubrolabiata* Fischer, 1902. VANUATU: BT-0100 and BT-5011 (Port Vila); BT-3493 and BT-3994 (off Banks Is.); BT-3959 (Vanuatu). *O. rufulogularia* Schepman, 1911. PAPUA NEW GUINEA (Rabaul): BT-3926, BT-3927, BT-4614, BT-4615, and BT-4616. *O. rufula* Duclos, 1835. PAPUA NEW GUINEA (Hansa Bay): BT-4599, BT-4600, BT-4601, BT-4602, and BT-4603. *O. sayana* Ravenel, 1834. U.S.A. (Florida, Marco Beach): BT-3012, BT-3013, BT-3105, BT-3108, and BT-3113. *O. scripta* Lamarck, 1811. HAITI: BT-3962 and BT-3964 (Gonave Bay); BT-2379 (off S coast). U.S.A. (Florida, Marathon Key): BT-2150 and BT-2154. *O. semmelincki* Schepman, 1911. PAPUA NEW GUINEA (Hansa Bay): BT-0793, BT-0794, BT-0795, BT-0796, and BT-0797. *O. sericea* Röding, 1798. INDONESIA (Bali): BT-0012, BT-0013, BT-2012 and BT-4046. NEW CALEDONIA (E coast): BT-3341. *O. sidelia* Duclos, 1835. SEYCHELLES (Mahé): BT-2707, BT-2708, BT-2710, BT-2712, and BT-2714. *O. spinicula* Röding, 1798. PANAMA (Cebaco Is.): BT-3765, BT-3766, BT-3767, BT-3768, and BT-3770. *O. splendidula* Sowerby, 1825. PANAMA (no loc.): BT-3729, BT-3731, BT-3733, BT-3736, and BT-3737. *O. taeniata* Link, 1807. THAILAND (Phuket): BT-0171, BT-1293, BT-1294, BT-1295, and BT-1298. *O. tessellata* Lamarck, 1811. PHILIPPINES (Sulu): BT-4508, BT-4509, BT-4510, BT-4511, and BT-4512. *O. tricolor* Lamarck, 1811. INDONESIA: DG-L15/10 (Flores, Awolong); DG-5326/14 (Bali); JS-026 and JS-027 (Java, Carita); BT-5015 (Tanimbar). *O. undatella* Lamarck, 1811. ECUADOR (San Pedro): BT-2681. MEXICO (Colima): BT-0331 and BT-0332. PANAMA (Venado Is.): BT-1665 and BT-1666. *O. vidua* Röding, 1798. INDONESIA (Bali): BT-0601. VANUATU: BT-0610 (Port Vila); BT-3312, BT-3313, and BT-3314 (no loc.). *O. williamsi* Melvill & Standen, 1897. MARSHALL IS. (Kwajalein): BT-2815, BT-2817, BT-2818, BT-2819, and BT-2820.

Genus *Olivancillaria*

O. contortuplicata Reeve, 1850. URUGUAY (La Coronilla): BT-1013, BT-1089, BT-1091, BT-5901. *O. ureus* Röding, 1798. BRASIL: BT-1073 (Sao Sebastiao, Praia do Paulista); BT-1079 and BT-1082 (Cabo Frio); BT-5867 (Rio de Janeiro). *O. uretai* Klappenbach, 1965. ARGENTINA (Monte Hermoso): BT-2877,

BT-2878, BT-2880, and BT-2881. *O. vesica vesica* Gmelin, 1791. BRASIL (off Rio de Janeiro): BT-1064, BT-1065, BT-1066, BT-1069, and BT-1070.

Subfamily OLIVELLINAE

Genus *Olivella* s.l.

O. anazora Duclos, 1835. MEXICO (Manzanillo): BT-5880 and BT-5881. *O. gracilis* Broderip & Sowerby, 1829. MEXICO (Nayarit): BT-5872, BT-5873, BT-5874, and BT-5875. *O. japonica* Pilsbry, 1895. JAPAN (off Mie Prefecture): BT-5885 and BT-5886. *O. pulchella* Duclos, 1835. GAMBIA (Cape St. Mary): BT-1716. SENEGAL (off Joal): BT-5878 and BT-5879. *O. volutella* Lamarck, 1811. MEXICO (Manzanillo): BT-0449. PANAMA (Pedro Gonzales Is.): BT-0641, BT-5876, and BT-5877. *O. zanoeta* Duclos, 1835. MEXICO (Manzanillo): BT-5887, BT-5888, and BT-5889. *O. zonalis* Lamarck, 1811. PANAMA (Isla del Rey): BT-0650 and BT-0652.

Subfamily ANCILLINAE

Ancilla (*Sparellina*) *acuminata* Sowerby, 1859. SOMALIA (no loc.): BT-1119, BT-1120, and BT-1121. *Ancilla* (*Sparellina*) *ampla* Gmelin, 1791. INDIA (off Madras, 10 fms.): BT-0527, BT-5925, and BT-5926. *Baryspira australis* Sowerby, 1830. NEW ZEALAND (no loc.): BT-2897, BT-2898, and BT-5902. *Ancillus buccinoides* Lamarck, 1803. (Fossil, Lutetian). FRANCE (Champagne, Damery): BT-5913, BT-5915, and BT-5919. *Ancillarina canalicifera* Lamarck, 1802. (Fossil, Lutetian). FRANCE (Champagne, Damery): BT-1208, BT-5903, and BT-5904. *Ancilla* (*Sarella*) *castanea* Sowerby, 1830. SAUDI ARABIA (Ras Tamura): BT-1133 and BT-1135. *Ancillista cingulata* Sowerby, 1830. W. AUSTRALIA (Onslow): BT-1646, BT-3230, BT-3231, and BT-3232. *Ancilla* (*cinnamomea*) Lamarck, 1801. INDIA (Cuddalore): BT-1127, BT-1128, BT-1129, and BT-1130. *Baryspira depressa* Sowerby, 1859. NEW ZEALAND (North Is., Waiki Beach): BT-2405, BT-2406, and BT-2407. *Amalda* (?) *dimidiata* Sowerby, 1850. This is the species illustrated pl.38, fig. 491 in RIOS (1985). BRASIL: BT-1049, BT-1050, and BT-1051 (off Itaipu, Rio de Janeiro); BT-5865 (off Santana, Rio). *Alocospira* (?) *edithae* Pritchard & Gatliff, 1898. S. AUSTRALIA (Coffin Bay): BT-1812, BT-1814, and BT-5920. *Eburna glabrata* L., 1758. VENEZUELA (no loc.): BT-0988, BT-5558, BT-5860, and BT-5864. *Eburna lienardi* Bernardi, 1821. BRASIL (Ceara, Acaraú): BT-0991, BT-0992, BT-0993, BT-0996, and BT-0997. *Ancilla* (*Sparellina*) *lineolata* A. Adams, 1853. ISRAEL (Eilat): BT-1143, BT-1144, and BT-1145. *Alocospira* (s.l.) *marginata* Lamarck, 1810. AUSTRALIA (Yorke Peninsula): BT-3274 and BT-3275; TASMANIA (Ulverstone): BT-3261. *Ancilla* (*Hesperancilla*) *matthewsi* Burch & Burch, 1967. BRASIL: BT-3497 and BT-3498 (Ceara, Fortaleza); BT-3499 (off Natal). *Alocospira* (s.l.) *monolifera* Reeve, 1864. W. AUSTRALIA: BT-1045 (Albany); BT-1047 (Busselton); BT-3269 and BT-3272 (Margaret River). *Ancillista muscae* Pilsbry, 1826. W. AUSTRALIA: BT-1051 (Exmouth); BT-1116 (no loc.); BT-3228 and BT-3229 (Onslow). *Gracilispira novaezelandiae* Sowerby, 1859. NEW ZEALAND (Mayor Is., 80 fms.): BT-2402, BT-2402a, and BT-2402b. *Ancilla* (*Sparellina*) *ovalis* Sowerby, 1859. KUWAIT (Fintas): BT-5921, BT-5922, and BT-5924. *Ancillus olivula* Lamarck, 1803. (Fossil, Lutetian). FRANCE (Champagne, Damery): BT-5905, BT-5907, BT-5909, and BT-5910. *Alocospira* (s.l.) *rosea* Macpherson, 1951. AUSTRALIA (Queensland, off Bushy Is.): BT-1801, BT-1802, and BT-1804. *Ancilla* (*Sarella*) *sarda* Reeve, 1864. TANZANIA (Zanzibar): BT-1705, BT-1706, and BT-1707. *Amalda tankervillii* Swainson, 1825. VENEZUELA (no loc.): BT-2319, BT-2320, BT-5890, and BT-5891. *Ancillista velesiana* Iredale, 1936. AUSTRALIA: BT-1669 (N.S.W.), Tweed

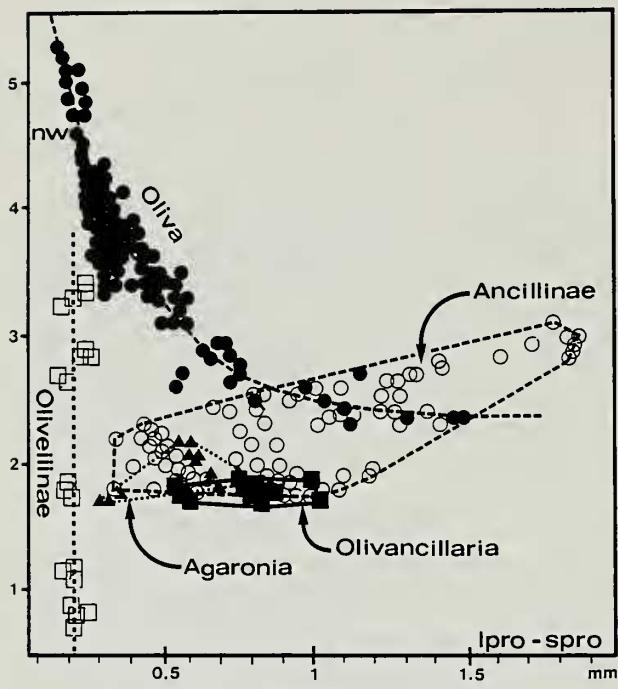


Figure 2

Family Olividae. Eighty-seven taxa. Scatter diagram of nw versus (lpro - spro).

Heads); BT-3224 (no loc.); BT-5868 and BT-5869 (Queensland, Moreton Bay). *Ancilla* (*Sparella*) *ventricosa* Lamarck, 1811. SOMALIA (no loc.): BT-1122, BT-1124, and BT-1125.

RESULTS AND INTERPRETATION

Figure 2 shows the distribution of all observed points in a scatter diagram of nw versus (lpro - spro). This would show correlations between the number of whorls of the protoconch and the rate of lateral expansion of its spiral. It will be noted that the distribution of *Oliva* (black circles) is not at all random: all specimens fall on a smooth, regular curve, as if obeying precise construction rules. Only a part of this curve overlaps the somewhat looser area of distribution of the subfamily Ancillinae (white circles).

Too few species of the subfamily Olivellinae and the genera *Agaronia* and *Olivancillaria* are represented here to secure firm conclusions. These groups will not be discussed any further but it will nevertheless be noted that the species of Olivellinae examined so far (open squares) have a quite distinctive distribution and fall approximately into a straight line, with little or no variation in (lpro - spro). *Agaronia* (black triangles) and *Olivancillaria* (black squares) are well grouped, overlapping each other as well as the margin of the Ancillinae (in the region of the genus *Ancilla*, cf. Figure 4) but quite separated from the Olivellinae and the genus *Oliva*. The subfamily Ancillinae and the genus *Oliva* will be examined separately in more detail hereunder.

Figure 3 shows the distribution observed for the subfamily Ancillinae in a scatter diagram of nw versus (lpro - spro). It will allow the identification of species in Figures

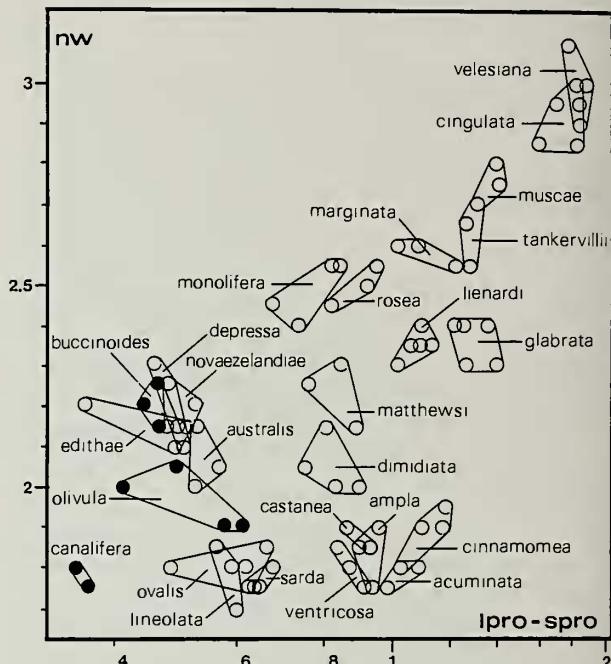


Figure 3

Subfamily Ancillinae. Scatter diagram of nw versus (lpro - spro). Grouping by species. Minimum convex polygons. Black circles: fossil species.

4 and 5. One can observe that species are very well grouped: the usefulness of protoconch measurements for species recognition and separation, already shown for *Oliva* (TURSCH & GERMAIN [1985]; see also Figures 6 and 7 in this paper) can thus be extended to Ancillinae.

Figure 4 also shows the distribution observed for the subfamily Ancillinae in a scatter diagram of nw versus (lpro - spro). It is on the same scale as Figure 3, on which species can be identified individually. One can notice that the species are not distributed at random and that the distribution reflects supraspecific groupings. One is tempted to interpret this graph in terms of phylogeny, as the distribution fans out from the more primitive, fossil species (black circles) in the lower left corner to the most advanced *Ancillista* in the opposite corner.

According to Dr. R. N. Kilburn (in litt.), "Amalda" *muscae* is in fact an *Ancillista* (fragile shell, large, bifid foot—an adaptation for swimming—and broad rachidian plate). Its position on the graph (see Figure 3) is thus quite logical.

It will be noted that *Ancilla matthewsi* is found to be well separated from the other *Ancilla*. Other important differences (unique, crenulated ancillid groove and atypical radula) have been noted for this shell by KILBURN (1981) who concluded (p. 357): "The possibility exists . . . that *matthewsi* is actually an offshoot of an *Amalda* or *Eburna* lineage" and created the subgenus *Hesperancilla* Kilburn, 1981, to accommodate that species. Dr. Kilburn recently wrote to me that it might be an idea to use *Hesperancilla*

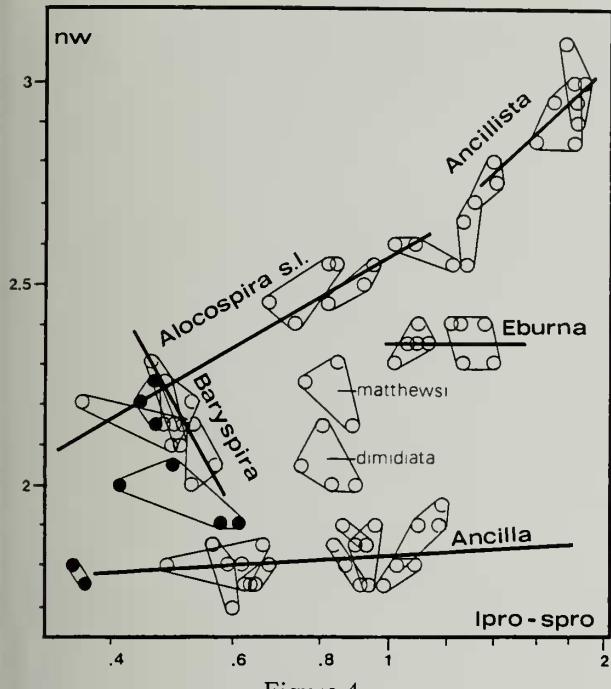


Figure 4

Subfamily Ancillinae. Scatter diagram of nw versus $(lpro - spro)$. Grouping by supraspecific taxa (for species identification, see Figure 3). Minimum convex polygons. Black circles: fossil species.

as a full genus. The generic position of *dimidiata* is still not clearly established. I cannot comment yet on its position on the graph.

Figure 5 shows the same data, on the same scale, but interpreted in terms of zoogeography. The coherent patterns that are observed are not surprising; for animals having a direct development (with reduced larval dispersal) one would expect related species to occur in the same or neighboring regions.

Figure 6 shows that when represented in the system of axes nw and $1/(lpro - spro)$ all specimens of *Oliva* are distributed along a nearly straight line. It will be noted that all 35 Indo-Pacific species examined (open squares) are closely grouped in the central part of the graph, in a range of values presumably close to the plesiomorphic (primitive) characters of the group. American and Atlantic species (black squares) are mostly found outside this zone (with the exception of *O. sayana* and *O. porphyria*).

Figure 7 is an enlargement of the "Indo-Pacific zone" of Figure 6. For the sake of clarity only 29 species have been represented. The missing species occur in the same general region as *Oliva caldania*. Here again it can be seen that intraspecific grouping is quite compact: most pairs of taxa can be unambiguously separated on the basis of only two protoconch characters.

DISCUSSION

From the data above, one can hardly escape the conclusion that protoconch measurements are meaningful at the su-

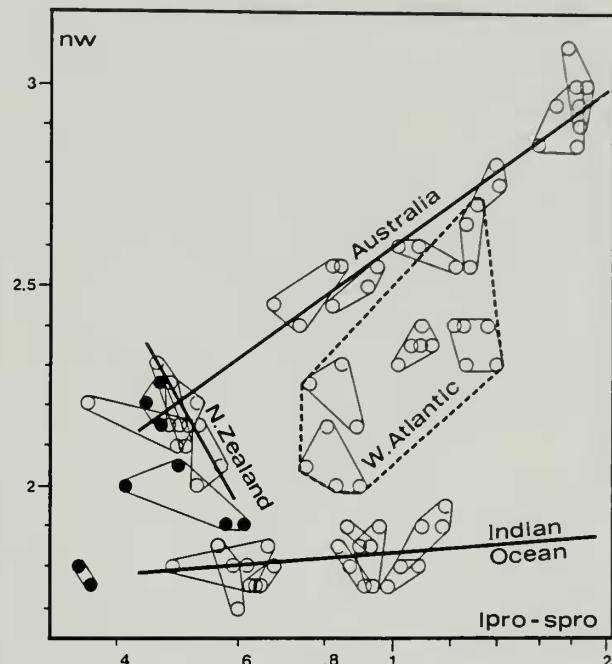


Figure 5

Subfamily Ancillinae. Scatter diagram of nw versus $(lpro - spro)$. Grouping by geographical distribution (for species identification, see Figure 3). Minimum convex polygons. Black circles: fossil species.

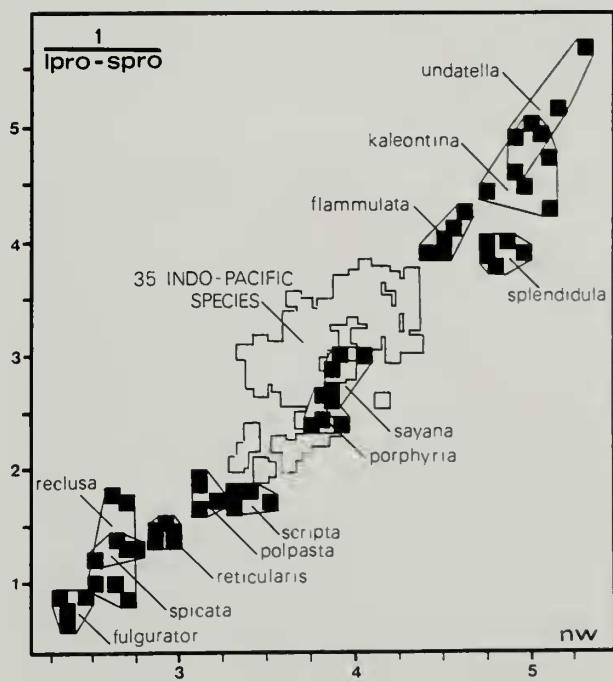


Figure 6

Genus *Oliva*. Scatter diagram of $1/(lpro - spro)$ versus nw . American and Atlantic species: black squares (minimum convex polygons). Indo-Pacific species: white squares (detailed in Figure 7).

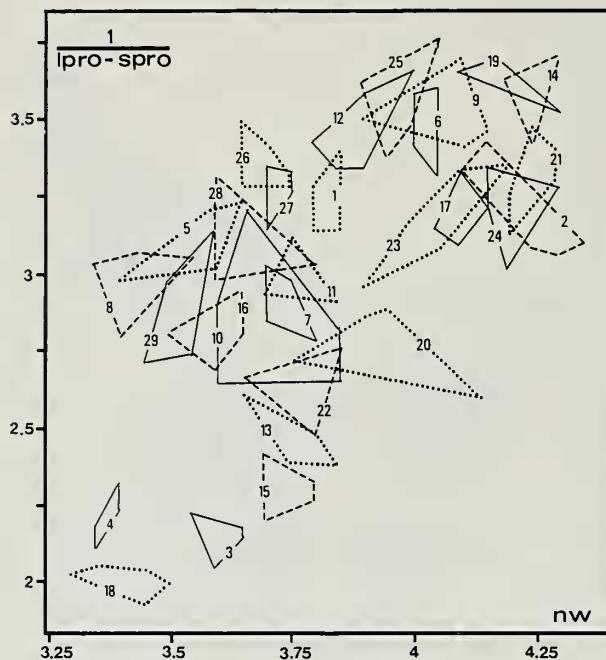


Figure 7

Genus *Oliva*: Indo-Pacific species (see text). Scatter diagram of $1/(lpro - spro)$ versus nw . Minimum convex polygons. 1: *O. amethystina*. 2: *O. arctata*. 3: *O. australis*. 4: *O. buelowi*. 5: *O. bulbosa*. 6: *O. bulbiformis*. 7: *O. caerulea*. 8: *O. caldania*. 9: *O. carneola*. 10: *O. caroliniana*. 11: *O. concinna*. 12: *O. dubia*. 13: *O. hirasei*. 14: *O. lacariantai*. 15: *O. lenhilli*. 16: *O. lignaria*. 17: *O. mantichora*. 18: *O. miniacea*. 19: *O. neostina*. 20: *O. ornata*. 21: *O. paxillus*. 22: *O. rufofulgurata*. 23: *O. rufula*. 24: *O. semmelinksi*. 25: *O. sidetia*. 26: *O. taeniata*. 27: *O. tessellata*. 28: *O. tricolor*. 29: *O. williamsi*.

praspécific level. There is a good agreement between the observed clusters of protoconch measurements and the commonly accepted supraspecific groupings (established on completely independent grounds).

There is no real contradiction between this conclusion and the statement of BOUCHET (1987:78; see also p. 109): "le mode de développement larvaire, et sa transcription dans la morphologie de la protoconque, ne traduit pas des liens de parenté et n'a aucune valeur taxonomique au niveau supraspécifique...." The author has carefully defined "mode de développement" as being the planctotrophic or non-planctotrophic modes of development and his negative conclusions are restricted to planctotrophic species, as clearly stated (p. 108): "En conclusion, les protoconques planctotrophiques ne constituent pas (pas encore ?) un outil classificatoire aux rangs supraspécifiques." This conclusion obviously does not apply to Olividae as these have a non-planctotrophic (intracapsular) mode of development (PETUCH & SARGENT, 1986) like the related family Volutidae (BOUCHET, 1987).

The spread of the different species in the graphs does not represent the real variability range, the randomly selected samples being far too small. In the cases for which

large samples have been examined (see for instance TURSCH *et al.*, 1986b) intraspecific variation remains small.

The striking regularities observed for the distributions of protoconch measurements in *Oliva* and *Olivella* do not necessarily have to be explained by direct adaptation; they might well reflect an architectural constraint in the building of these particular types of protoconchs (see GOULD & LEWONTIN, 1978).

It is very unlikely that protoconch shape and size would be dependent on local ecological factors alone. For instance, *Oliva spicata* and *O. kaleontina* have very dissimilar protoconchs and yet can be found side by side in the Panamic region. An interpretation in terms of phylogeny seems more plausible.

I do not advocate here a supraspecific classification of Olividae based upon protoconch characters alone. Furthermore, great caution should be exerted in the interpretation of the data hereabove because coincidence of points in the graphs does not necessarily imply identity of protoconch types. Proper representation of protoconch morphological trends requires a multidimensional space (with as many reference axes as there are characters to be taken into account). In bi-dimensional graphs such as those presented here, constellations of neighboring points (just like constellations of stars) can include objects separated by large distances along another dimension. It should be remembered that nw , $lpro$ and $spro$ do not determine the shape or the size of the protoconch. As an example, the protoconchs of *Eburna glabrata* and of *Oliva fulgorator* have similar values for nw and $(lpro - spro)$ but are very dissimilar in other aspects.

Much additional work is required for the exploration of the 10 other protoconch variables defined in TURSCH & GERMAIN, (1985, 1986a). Research along these lines is being actively pursued in this laboratory.

ACKNOWLEDGMENTS

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